Animal Pollinators and their Food Plants along Latitudinal and Climatic Gradients in South American Lowland Forests

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For my parents and grandma, Miriam, Christian and Carolin, with love

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Introduction

Plant-pollinator interactions have fascinated natural scientists since a long time (e.g., Köhlreuter 1761, Darwin 1859, Wallace 1867). Due to the omnipresence in everyday life especially rural people have realized the importance of animal pollinators since the antiquity. In ancient Egypt 2000 B. C. people realized the connection between visits of honey bees and an increase of fruit production in their plantations (http://www.lwg.bayern.de/analytik/honig/linkurl_2.pdf). The observations of animal pollination have been quantified in modern times. Klein et al. (2007) reported that in Europe 84 % and in the tropics 70 % of all crop species are pollinated by animals. In natural ecosystems the rate of animal pollination can even be higher. Bawa (1990) reported for tropical lowland rainforests that up to 99 % of all plant species are dependent on animal pollination. Thus, pollination services provided by animals can be seen as an essential ecosystem service. Here I contribute to our growing knowledge of patterns of pollinator diversity in the Neotropics and the understanding of ecological factors influencing it. My thesis encompasses analyses of patterns of species richness and assemblage composition of three pollinator groups (bees and wasps, butterflies, hummingbirds) along latitudinal and climatical gradients and relates them to food and climate related factors.

Tropical areas host a large variety of diurnal and nocturnal pollinator groups. The main diurnal groups in South America are bees and wasps, flies, beetles, butterflies, and hummingbirds. At night, they are mainly replaced by moths and bats. Nonetheless, bees are the most important pollinators worldwide (Fleming and Muchhala 2008). Van Dulmen (2001) reported that 54 % of all plant species in two Amazonian rainforests are pollinated by bees.

Most bees and almost all wasps (Fig. 1a) have short tongues, which only enable them to feed from relatively unspecialized, open flowers providing nectar and/or pollen. Several larger bee and bumblebee species have long tongues, which enable them to feed from more specialized, often larger flowers. These flowers mainly provide larger quantities of nectar and hide it in long corolla tubes or nectar spores, which small bees can not reach (Proctor et al. 1996). Sometimes those plant species even prevent smaller bee and wasp species that do not act as effective pollinators from entering by mechanical barriers, which only larger and stronger bee species can open (e.g., *Lupinus ssp.*, Fabaceae; *Salvia pratensis*, Lamiaceae). A few plant species do not provide nectar or pollen as the main reward for pollinators but fatty, sometimes aromatic oils. Some of the most famous ones are the Neotropical orchids in the subtribes Stanhopeinae and Catasetinae (Williams and Whitten 1983). They are exclusively visited by male orchid bees (Euglossini; Fig. 1c), which collect the aromatic substances to mix a species specific perfume in grooves of their enlarged hind legs to attract females for mating. In addition to this behavior all orchid bees also visit flowers with long corolla tubes to feed on nectar. Surging for aromatic substances and nectar orchid bees fly large distances, which makes them to effective, long distance pollinators (Janzen 1971).

Another important group of pollinators are butterflies (Fig. 1b). The majority of all butterfly species act as pollinators by feeding on nectar and in a few cases also on pollen (Gilbert 1972). The others, mainly tropical species feed on decaying fruits, carrion, dung, or do not feed at all as imagines. In contrast to bees, which feed themselves and their offspring with pollen and nectar, butterflies only feed on floral rewards as adults. Their larvae feed on non floral plant tissues. Similar to bees, butterfly species have proboscises of different length (Proctor et al. 1996). Butterfly species with a short proboscis feed on smaller, relatively open flowers whereas species with a long proboscis feed on flowers with longer, often very narrow corolla tubes (e.g., *Ixora spp.*, Rubiaceae).

Plant species adapted to pollination by one of the two mentioned insect groups always offer landing platforms for the pollinator, which enables the pollinators to sit on the flower during feeding. In some cases plant species adapted to butterfly pollination developed

strongly elongated styles and filaments the butterflies touch with their wings during landing on the flower (e.g., *Caesalpinia pulcherrima*, Fabaceae). The positioning of pollen on the butterfly´s wings by these plant species increase the chance of pollination because the butterflies constantly move their wings during feeding and thus dispense the pollen on the style (Cruden and Herrmann-Parker 1979). Due to their often long and flexible proboscis butterflies are known to be opportunistic in their food choice (Tudor et al. 2004). They often visit flowers showing typical adaptation to bird pollination to drink from the rich nectar resources. Independent of the flower morphology butterfly pollinated plant species often have conspicuously red or pinkish flowers, which makes the flowers easily recognizable against a green background. Instead, mainly bee pollinated plants often have white, yellow or bluish flowers because bees in contrast to butterflies are not able to see red colours (Ilse 1941).

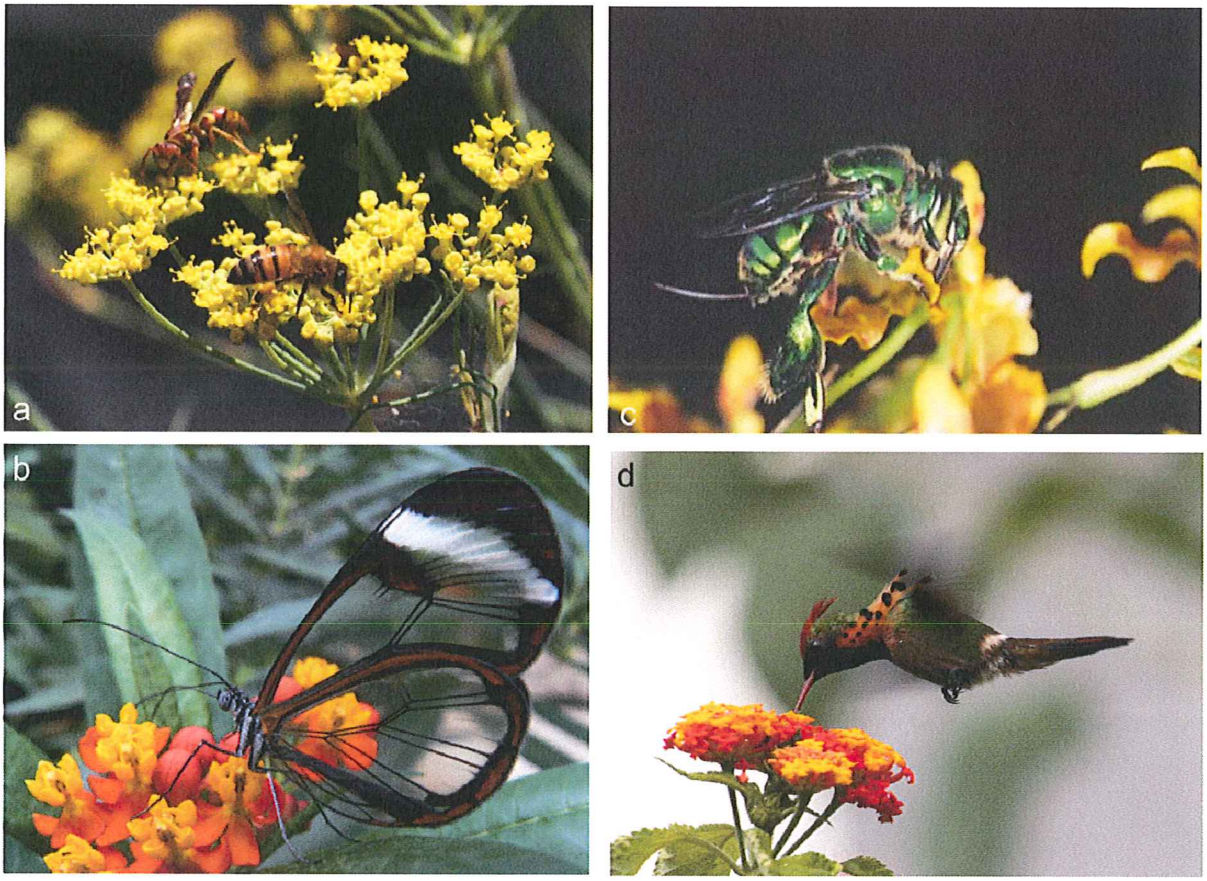

Figure 1: Pollinator groups which have been studied: a) Bees and wasps, photo from www.roundrockgarden.com, b) Butterflies, photo from www.picturesnob.com, c) Orchid bees, photo from www.arcticphoto2.co.uk, d) Hummingbirds, photo from www.pbase.com; For the analyses orchid bees have been included into the category bees and wasps or analysed separately in studies excluding the other groups.

Not just insects but also vertebrates are an important group of pollinators in some parts of the world. Vertebrates, mainly birds and bats but also a few mice and geckos, pollinate between 3-11 % of the local flora in the tropics and subtropics (Devy and Davidar 2003), with values in south-western Australia of up to 15 % (Keighery 1980). Vertebrates normally have larger home ranges than insects, which increase their effectiveness as pollinators because they carry pollen from a higher number of plant individuals, which increases the outcrossing rate of the pollinated plants (Faegri and van der Pijl 1966). But for a plant species it is also more cost intensive to attract vertebrate pollinators because vertebrates need a higher amount of energy to fulfil the energetic demands of their homoiotherm bodies than insects (Faegri and

van der Pijl 1966). Thus, vertebrate pollinated plant species need to invest more energy in the production of rewards to attract their pollinators. Therefore, in almost all habitats the majority of plant species is pollinated by insects.

While in tropical lowland rainforests bats are the most diverse vertebrate pollinators the importance of birds as pollinators increases with increasing elevation (Proctor et al. 1996). In the Neotropics hummingbirds (Fig. 1d) are the most species rich nectarivorous birds (Schuchmann 1999). They are highly specialized on nectar. The surge for nectar requires 85-90 % of their daily foraging effort (Gass and Montgomerie 1981). In contrast to bats, which are active during the night, hummingbirds are able to fall in torpor at night, which means they reduce all body functions to a minimum to save energy. But if the nights are too cold bats spend more energy than they can absorb by drinking nectar. Thus, this mechanism limits the elevational distribution of nectarivorous bats but not of hummingbirds (Dobat and Peikert-Holle 1985).

The flowers hummingbirds typically visit are conspicuously coloured, often red or orange, have a long corolla tube and produce high quantities of sucrose rich nectar (Buzato et al. 2000). It is well known that the morphology and physiology of hummingbird species are strongly related to flower morphology and nectar production of their food plant species (e.g. del Coro Arizmendi and Ornelas 1990, Cotton 1998). Normally, long-billed hummingbirds visit flowers with long corolla tubes, while short-billed species visit flowers with shorter corolla tubes. However, several recent studies have documented that many hummingbird species also visit flowers that morphologically do not appear to be suitable food plants (e.g., Dziedzioch et al. 2003, Lara et al. 2009). Especially during times of low food abundance, generalistic medium sized hummingbird species with relatively short bills use small, insect-pollinated flowers opportunistically to cover their energetic demands (e.g. Stiles 1978, Araujo and Sazima 2003).

As mentioned before the three groups of pollinators are dependent on nectar and/or pollen as food resource. But it is known that in general not only food related but also climate related factors influence the diversity of species. Actual evapotranspiration (AET), a measure used as a surrogate for energy availability combining temperature and rainfall, is often positively related to species richness (Wright 1983). Climatic factors can influence species richness directly or indirectly via the availability or diversity of food resources. Much of this argument revolves around the idea that climatic conditions influence ecosystem productivity. Therefore, ecosystems with higher productivity have quantitatively and qualitatively more resources that can be partitioned onto consumer species (Evans et al. 2005). Evans et al. (2005) reported several, partly contrasting mechanisms how species richness is effected by energy availability in an ecosystem.

In my thesis, I tested the following factors, which are partly combinations of the mechanisms of Evans et al. (2005):

1. Resource abundance: With increasing productive energy an area can provide more resources and thus supports a species assemblage of more individuals of a given group of species. The individuals of a species assemblage are comprised of individuals randomly selected from the regional species pool. If more individuals are selected the chance of adding new species increases. Therefore, along a gradient of increasing productive energy the number of individuals and species of a given group should increase.

2. Resource diversity: With increasing productive energy in an ecosystem the available amount of resources increases as well as the diversity of resources. Therefore, relatively rare resources become more abundant. Those former rare resources can be used by niche specialists and therefore the species richness within the species assemblage increases. In general the increase of resource diversity enables the more generalistic species to switch to less intensively used resources and decreases competition which increases species diversity (Evans et al. 2005).

3. Climatic conditions: If temperature increases in an ecosystem the climatic conditions can fall in the tolerance range of more species, which increases species richness (Evans et al. 2005). Especially the diversity of poicilotherm organisms is negatively influenced by low minimum temperatures. For example along a gradient of increasing minimum temperatures the diversity of butterfly species increases (Hawkins and DeVries 2009).

The work presented in this thesis is part of a series of studies investigating the patterns of pollinator diversity and the environmental factors determining it. The influence of some single factors on the diversity of individual pollinator groups has either been analysed on a very large, continental scale (e.g., Rahbek and Graves 2000, Michener 2000, Hawkins and DeVries 2009) or on a very small, local scale (e.g., Potts et al. 2003, Cotton 2007). On a large scale bees are known to be more diverse in warm, temperate, and xeric regions than in the humid tropics (Michener 1979, 2000), presumably reflecting their physiological and behavioural adaptations. Instead, on a local scale both the number of flowers and the number of plant species determine the species richness of bees (Potts et al. 2003). Orchid bees are an exception among bees. Distributed from southern Arizona and Texas to Paraguay and northwestern Argentina (Moure 1967, Minckley and Reyes 1996) they are most diverse in tropical lowland and low montane forests (Roubik and Hanson 2004) where they presumably can find the highest diversity of plant species providing aromatic substances. Butterfly diversity is negatively influenced by frost events (Hawkins and DeVries 2009). Therefore, butterflies diversity increases with increasing minimum temperatures in single localities (e.g., Pozo et al. 2008) or along climatic gradients (Hawkins & DeVries 2009). Just a few studies have so far been able to demonstrate that nectar resources have a significant effect on the diversity or abundance of butterflies (Hill 1992, Steffan-Dewenter and Tscharntke 1997). Instead, hummingbirds are most diverse in montane forests (Schuchmann 1999). Due to the ability to reduce their energy demands during the night and to fly also during times of cool and moist weather hummingbirds are very reliable pollinators in those habitats. Towards the lowlands the hummingbird diversity decreases especially towards areas with a marked climatic seasonality (Rahbek and Graves 2000), presumably because nectar resources become scarce during parts of the year. On a local scale several studies showed that hummingbird abundance is strongly related to the availability of food (Araujo and Sazima 2003, Cotton 2007). Despite much important progress, a gap remains regarding our understanding of which biotic or abiotic factors determine the diversity patterns of different groups of pollinators on a larger scale. At the background of a predicted increase of climatic seasonality and a decrease of precipitation in central South America in the next 100 years (Christensen et al. 2007) it is especially important to know, which environmental factors determine pollinator diversity to be able to protect them because they offer one of the most important ecosystem functions.

In this context and on the background the mechanisms described by Evans et al. (2005), the main contribution of my thesis has been to analyse the impact of biotic and abiotic factors on the diversity and distribution of pollinators in central South America. I tried to analyse the different patterns on different taxonomic scales and by using different sets of environmental factors. As an example of a small taxonomic group I conducted a study on the climatic and edaphic factors determining the diversity of orchid bees along a latitudinal gradient form the Equator to the subtropics (Chapter 2) and analysed seasonal changes of aromatic preferences by orchid bees (Chapter 3). Those two studies were contrasted by a large study, in which I analysed a set of biotic and abiotic environmental factors determining the diversity patterns of three different groups of pollinators (bees and wasps, butterflies, hummingbirds) and the relations between the different groups on a regional scale (Chapter 5 and 6). Further, in the background of the predicted increase of climatic seasonality and the decrease of precipitation in central South America I analysed the turnover rate of pollinator groups and their food plants between adjacent sites to find out how diversity patterns of

pollinators are connected to the diversity patterns of their food plants (Chapter 4). And at least, I tested the effectiveness of different coloured pan traps to collect bees and wasps in different forest types (Chapter 1).

In **Chapter 1** I investigate whether blue or yellow pan traps are more effective to sample bees and wasps in tropical and subtropical forests along a latitudinal, climatic, and forest structure gradient. This issue becomes important when studies on the diversity of bees and wasps in tropical forests are planed. The effectiveness of pan traps has only been investigated in openland habitats in the temperate regions. But the technique has also been used in tropical forests. In forests the different canopy covers could influence the effectiveness of traps compared to openland habitats because of a different microclimate, which could influence the assemblage composition of bees and wasps. Further, different coloured traps could attract different families of bees and wasps dependent on the canopy cover, precipitation regime, climatic seasonality and latitude. To test for the effect of canopy cover I also collected bees and wasps at the forest margins. Thus, I investigated the effectiveness of different coloured pan traps in different types of forest and at forest margins along a gradient of latitude and climatic factors (precipitation and climatic seasonality). Overall, I found that yellow traps collected more individuals than blue traps. Blue trap did not collect more individuals or species of any family of bees and wasps than yellow traps. Yellow traps collected significantly more individuals of Ichneumonidae, Nyssonidae, Pompilidae, and Crabronidae than blue ones. With increasing canopy cover the effectiveness of blue traps declined compared to yellow traps. Further, the collected number of bee and wasp individuals increased from the tropical to the subtropical sites. This trend was mainly driven by Crabronidae, Halictidae, and Vespidae, whereas Ichneumonidae showed the opposite pattern. Indeed, the increase in bee and wasp density went parallel with a decline in canopy cover and climatic seasonality but when I took in consideration collection density data of bee and wasps individuals inside the forest and at the forest margin I found no difference. Thus, the observed latitudinal increase of bee and wasp density was more determined by geography and climatic seasonality. Instead, the decrease of the effectiveness of blue pan traps compared with yellow traps is related to an increase in canopy cover. Probably, the yellow traps are more conspicuous and thus attractive in shady forests compared to the blue ones. In conclusion, a combination of different coloured pan traps are useful to sample bees and wasps in tropical forests. But due to taxonomic colour and habitat preferences, regional shifts in family composition of the assemblages, and regional and local changes in vegetation structure especially studies along strong ecological or geographical gradients have to be planed, and the results have to be interpreted with care.

In **Chapter 2** I investigate patterns of orchid bee diversity and assemblage composition along a latitudinal gradient from the Equator to the subtropics and the environmental factors related to it. For Amazonia only a few studies on large scale diversity patterns on animals, especially insects have been conducted, yet. The region is famous for its species richness, for example of pollinators. Bees are the most important pollinators in the Neotropics such as in many areas of the world. Generally, bees are most diverse in temperate, xeric and warm areas and become less species rich towards the humid tropics. Orchid bees are an exception from this pattern. They only occur in the Neotropics and are most diverse in lowland and lower montane rainforests of Central and South America. Due to their long tongues and their ability to fly long distances they are important pollinators of several specialized bee pollinated plant species. Further, male orchid bees exclusively visit some plant species, for example up to 650 orchid species to collect aromatic substances. Those substances are used to create 'perfumes', which attract female orchid bees for mating. Their distribution pattern and ecological importance make orchid bees a particularly interesting group for biogeographical studies. I studied the orchid bee diversity and assemblage composition along a latitudinal transect of more than 2000 km from tropical Peru to the

subtropical Gran Chaco region in Bolivia and related environmental factors to the observed pattern. Further, I searched for indicator species for the different biogeographical zones by Species Indicator Analysis. I found that species richness and assemblage composition were mainly related to precipitation such as to climatic seasonality. Also, some edaphic factors were significantly related but they only have an indirect effect on orchid bee assemblages via their relationships to plant communities and habitat structure. The Species Indicator Analysis and the DCA (Detrendent Correspondent Analysis) revealed evidence for three biogeographical zones, subtropical Bolivia, tropical Bolivia and Peru. Tropical Bolivia can be seen as a transition zone between the species poor subtropical assemblages, occurring in deciduous dry forests with a marked climatic seasonality and the species rich Peruvian assemblages occurring in evergreen tropical rainforests without a marked climatic seasonality. In conclusion, climatic factors and the vegetation types strongly influence the distribution of orchid bees and their assemblage composition. But, whether the diversity of orchid bee assemblages is directly related to climatic conditions or other, proximal factors such as the availability or diversity of food plants or plant species providing aromatic substances cannot be answered with the data available at present. Also historic or evolutionary causes could influence the current diversity pattern.

In **Chapter 3** I investigate ecological applications of seasonal changes in odour preferences by male orchid bees. Male orchid bees visit a large variety of flowers and other odour sources to collect aromatic substances. These substances are not eaten but stored in pockets of the males hind tibias. Each species collects a species specific set of aromatic substances and uses it as a perfume to attract females for mating. The composition of aromatic substances is relatively stabile between populations of the same species, but variation can occur if a population exists on a small island for example. Also variations of odour preferences between seasons have been reported. These variations between seasons are only known for some species of orchid bees. But the distribution patterns of those species and the proportion of species with seasonal changes in their odour preferences within orchid bee assemblages, is not known yet. Also the environmental factors, which are related to the species distribution patterns are unknown. Therefore, orchid bees are a good model group to study how organisms change their utilisation of resources between seasons along a gradient of climatic seasonality and precipitation, how this relates to environmental factors, and which ecological implication the change has for the organisms. To investigate this I surveyed odour preferences between seasons of orchid bee assemblages along a 380 km gradient of climatic seasonality and precipitation in Bolivian lowland forests. I found that within an assemblage the proportion of orchid bee species that show odour preference changes between seasons, increased from north to south related to an increasing climatic seasonality. This pattern is interpretable in two not contradicting ways. First, it is likely that climatic seasonality mainly affects the orchid bees via a temporal turnover of aromatic substances provided by the plants. Plant phenology is well known to be strongly determined by environmental factors. Plant species in climatically more seasonal sites tend to synchronise their flowering phenology more strongly than in climatically non-seasonal sites. Thus, the southwards increasing proportion of orchid bee species that change their aromatic preferences between seasons within the assemblages may mainly be an opportunistic reaction to the increased seasonal turnover of a limited number of aromatic substances provided by the plants towards the south. Second, the vast majority of orchid bee species that showed changes in their odour preferences belonged to *Euglossa* subgenus *Euglossa*. I therefore suggest that the ability to change in the aromatic preference between seasons can be interpreted as a pre-adaptation that enabled species of this subgenus to colonize climatically strongly seasonal habitats.

In **Chapter 4** I investigate the degree to which the assemblages of pollinators and their food plants shift in response to climatic seasonality along a latitudinal gradient to evaluate the specificity of plant-pollinator relationships. Especially in tropical forests, the environmental

factors determining the assemblage composition of pollinators are poorly understood. For central South America climate models predict an increase of climatic seasonality and a decrease of precipitation. Therefore, plant assemblages will shift in the future. The impact of this shift on the pollinator assemblages are unknown, yet. Due to the enormous importance of pollinators for ecosystem functioning, this question has a high priority for natural ecosystems as well as for agricultural systems. Therefore, I analyzed the species turnover rate of three groups of pollinators, bees and wasps, butterflies, and hummingbirds and their food plants along a gradient of climatic seasonality and precipitation in Bolivian lowland forests. I found that the species turnover of food plant assemblages between adjacent sites was much stronger than that the species turnover of pollinator assemblages in the different pollinator groups. The seasonal changes in pollinator assemblages and their food plants were mainly determined by temperature and precipitation seasonality (Fig. 2, right column). However, the species composition within the assemblages of the different pollinator groups did not change strongly between seasons whereas the species abundance changed strongly in the assemblages of pollinator groups. Some reasons for this are regional migrations, food storage, and outliving harsh conditions in larval stages. The results suggests that pollinators are geographically more evenly distributed than their food plants, which implies that there is only low specificity between pollinators and their food plants. It is likely that in the future pollinator assemblages will flexibly react to climate change by shifts in species abundances and in their choice of food plant species. Thus, new plant-pollinator relationships will develop in natural systems. What will happen in agricultural systems is even harder to predict because land use is by far the most important reason for disruptions in plant-pollinator relationships and the decline in pollinator diversity.

In **Chapter 5 and 6** I investigate the influence of climatic, edaphic and food related factors on the diversity patterns of three groups of pollinators along a latitudinal gradient in Bolivian lowland forests. Further I analysed the relations between pollinator groups along the gradient. The Neotropics are inhabited by a rich pollinator fauna. Many different groups of insect and vertebrate pollinators are known for this area. But the biotic and abiotic factors determining the diversity within the different pollinator groups are poorly understood, especially on a larger scale. Climate and food related factors are known to have an influence on pollinator diversity. However, their impact on a larger scale, remain vague. Further, the relations in species numbers between pollinator groups have not been analysed, yet. It might be possible that insect pollinator groups compared to hummingbirds are more diverse in climatically more seasonal areas due to their ability to outlive periods of unfavourable conditions in larval stages. Further, hummingbirds might be more diverse in areas with a very high amount of precipitation because they are able to fly during humid periods in contrast to insects. To solve those questions, I studied diversity patterns of three groups of pollinators, bees and wasps, butterflies, and hummingbirds and related their species numbers to biotic and abiotic factors in a first step. In a second step I tested whether the diversity pattern of the individual pollinator groups vary between seasons. In a last step I related the diversity patterns of the pollinator groups to each other to see whether relations between the groups exist. I found that the diversity of bees and wasps was mainly related to the diversity and abundance of food. The diversity of hummingbirds was mainly related to the continuous availability of food. Instead, the diversity of butterflies was related to air temperature (Fig. 2, left column). Only the species number of butterflies differed significantly between seasons. Shifts in the proportion of pollinator group diversity did not occur along the study gradient. Instead, the species proportions between the different pollinator groups remained constant along the latitudinal gradient. In conclusion, the diversity of each pollinator group showed different patterns along the climatic gradient and was related to different environmental factors. Summarising the published results, the factors relating to the diversity patterns of the different pollinator groups appear to be the same worldwide, regardless of the habitat type or the

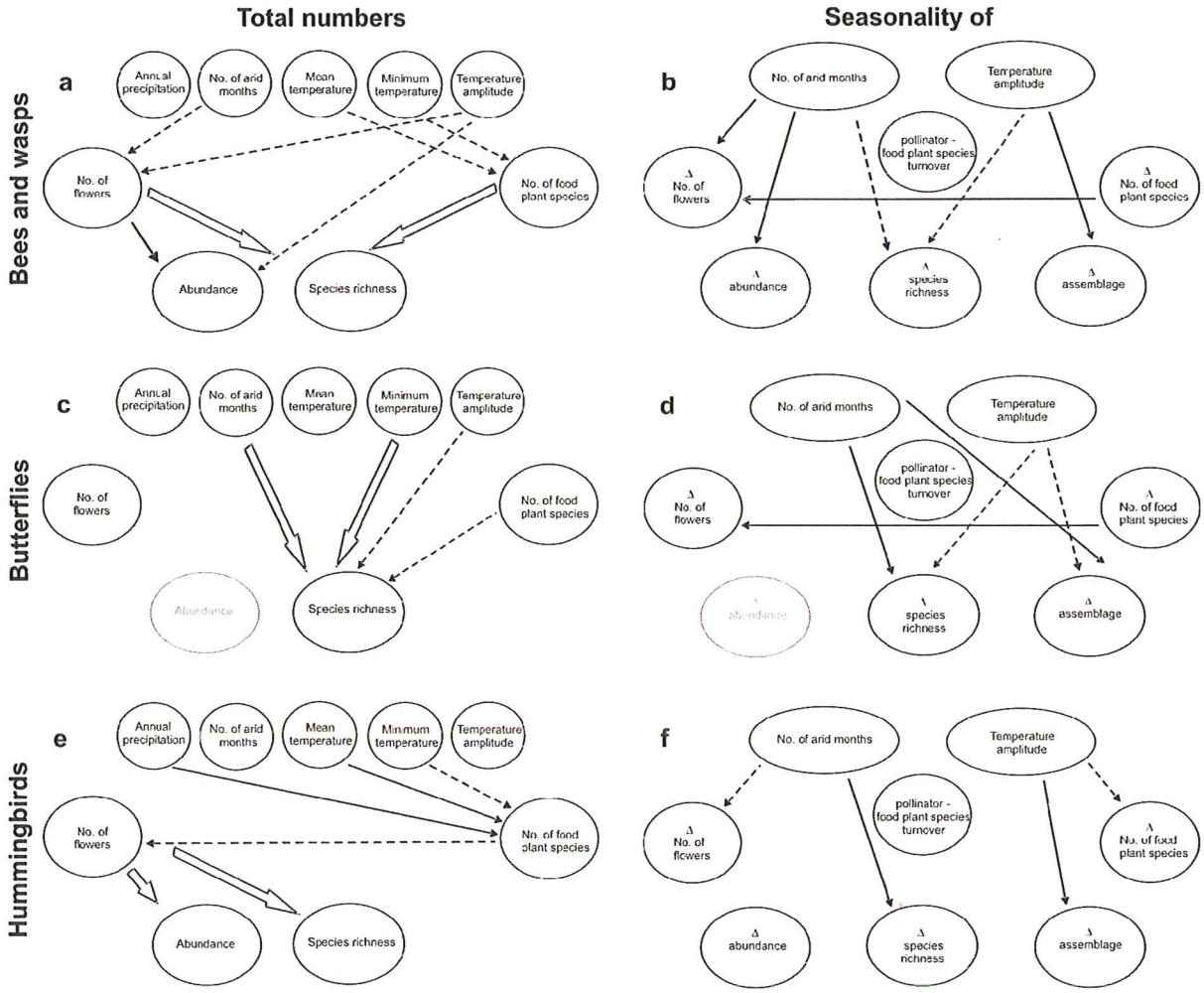

Fig 2.: Simplified relations between pollinator groups and environmental factors studied in Chapters 4-6; broad arrows: strong relations, continuous arrows: medium relations, dashed arrows: weak relations.

geographic latitude. In my study also the proportion in species numbers between pollinator groups remained constant along our gradient from subtropical, deciduous forests to tropical, evergreen rainforests. These results are especially surprising because the diversity of the different groups is related to different environmental factors.

As a general conclusion, my thesis demonstrates that each group and subgroup (orchid bees) of pollinators has a very specific ecology. The diversity of each of the three groups of pollinators is related to specific environmental factors but the different groups are quantitatively related to each other along the latitudinal gradient (Chapter 5 and 6). Thus, a common environmental factor organizing the relation between the groups must exist. Surprisingly, the diversity of orchid bees was related to different environmental factors than the diversity of the rest of the bees and wasps (Chapter 1 and 2). Probably, due to their very special behaviour orchid bees, as a highly tropical group of organisms are an exception among bees (Chapter 2 and 3). However, the relations of the pollinator groups to their food plants appeared to be surprisingly weak, which will lead to the development of new plant-pollinator relations during climate change (Chapter 4).

This thesis raises a suite of further questions. For example, beside its relation to climatic factors is the diversity of orchid bees also related to the abundance and/or diversity of

food plants and/or sources of aromatic substances? Maybe climatic factors mainly affect the abundance and/or diversity of food plants and/or sources of aromatic substances of orchid bees. The relatively low diversity and occurrence of mainly generalist orchid bee species in the two most southern, subtropical sites indicates this.

Is the quantitative proportion of the three groups of pollinators fixed in tropical mainland rainforests in South America, and if so, which environmental factors determine this relation? In a study on pollinator groups on different Caribbean islands a similar but weaker quantitative relation was found, as well. But on islands the set of pollinators is known to be reduced compared to the mainland. This reduction could be developed differently in the three pollinator groups. Thus, due to the small island size and its position far away from the cost the studied systems are difficult to compare with mainland systems.

How common are regional scale latitudinal and elevational migrations of butterflies and hummingbirds to avoid unfavourable environmental conditions? My studies revealed that some hummingbird and butterfly species conduct latitudinal and regional migrations but it remained unknown how many species regularly migrate and in which quantity. If several montane species for example regularly migrate downwards in larger quantities during the dry season to escape from cold weather the destruction of lowland forests would lead to the extinction of several montane species, as well.

The three mentioned questions can convey an impression how diverse the open questions regarding the ecology and distribution of South American pollinators still are. This thesis should just be seen as a first step in documenting and analysing large scale ecology and distribution of pollinator groups in the Neotropics. Therefore, I hope my thesis will have lasting impact in the understanding of diversity patterns and ecology of Neotropical pollinators and inspire similar studies to solve the remaining, open questions. Further, I hope that my results will help to protect the remaining Bolivian lowland forests, which would give the plant and animal species the chance to survive the challenges of climate change. Finally, I hope that you will enjoy reading this thesis.

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